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SEASONAL ABUNDANCE OF THE MOSQUITO DESTROYING TOP-MINNOW, GAMBUSIA AFFINIS, ESPECIALLY IN RELATION TO MALE FREQUENCY

R. L. BARNEY

Director, U. S. Fisheries Biological Station, Fairport, Iowa

AND

B. J. ANSON

Scientific Assistant, U. S. Bureau of Fisheries

The problem of mosquito larval control by the use of the viviparous top-minnow, *Gambusia affinis,* requires consideration of three important factors which must be dealt with in any attempt at biological control of immature mosquitoes. The first factor is an upset in the balance of nature of a mosquito-infested pool whereby certain components of the complex ecological association in which anopheline and other mosquitoes find their habitat are "so varied as to weaken either the means of defense of the mosquitoes or strengthen the offensive of their enemies." This upset of the equilibrium of the plant and animal associations of the pool is doubtless of chief importance in effecting a "natural" control. And this with reason; for fishes and mosquito larvae have been cohabitants of the same environmental area for ages, and there has been evolved such a neutralization between overproduction of mosquitoes and all repressive influences that both mosquitoes and fishes may be expected ordinarily to be found in any pond. Mosquitoes are normally able to maintain their numbers notwithstanding the controlling influence of fishes and other enemies. This required upset in the environment should tend toward the presence in larger numbers or quantities, absolutely or effectually, of those members or factors of the given association which are inimical to mosquito larval life but whose inimical effect has been counteracted heretofore by one or more other elements of the environment. This variation in the kind and amount of certain constituents of the ecological association under consideration can be brought about mechanically, e.g., by damming, deepening, straightening the banks of, or by causing a current to flow through the body of water. The introduction of certain chemicals may also serve to unbalance the equilibrium of nature. Then again, the upset may be brought about quite as easily biologically by the introduction of such plants and animals as may best serve the purpose.

The second important factor in biological control is the presence in the environment of an abundance of the top-minnow, the mosquito enemy on which the biological control theory may be based. The planting of *Gambusia* in a mosquito-infested pool after its existing equilibrium of plant and animal life has been overbalanced is analogous to the law of mass action. It means a permanent presence of the enemy fish in such numbers as the water can support. It means too that reversibility to the previous condition of equilibrium in which the mosquito larvae were able to maintain themselves cannot soon occur again.

The third important factor in biological control of the mosquito larva and pupa, based on the top-minnow as the actual destructive agent, is the elimination of fish and other animals predaceous on the minnow; or, if this is impracticable, the protection of the minnow from its enemies by the provision of shallow water margins. The effect of predaceous fish on the abundance of the minnow is considerable, and, as will be pointed out, the greatest loss of the minnows from this cause occurs when mosquito egg deposition is still abundant in September and October.

The effectiveness of the top-minnow depends then entirely on the conditions under which it lives. The production and availability of and the competition for food may be such as to limit the potential breeding of the minnow; the habits of growth of aquatic plants may physically reduce the fish's effectiveness as a control agent and at the same time so modify the environment that the minnow's prolificness is destroyed; the presence of lifeless materials in the water may serve as obstructions to the fish and as protection to the larvae; the minnow's enemies may bring to bear considerable influence to decrease the abundance of the fish and therewith the effectiveness of the species. The number and complexity of the various influencing factors for or against biological control of immature mosquitoes may accordingly be many. It has been pointed out,[1] however, that the environmental features of a body of water may be easily changed so that whatever effectiveness *Gambusia* may have as a larval control agent may be considerably magnified.

The preparation of the ponds as outlined in the reference cited above required such physical and biological changes as would tend naturally toward an increase in the number and effectiveness of *Gambusia* and the protection against or elimination of predaceous fish. These two factors may well be taken care of mechanically. The provision of an abundance of *Gambusia* is, for the most part, however, a matter in which environmental factors as well as inherent characteristics of the fish probably play a part. It appears that the abundance and prolificness of *Gambusia* varies locally and also seasonally; and this fact, considered from the viewpoint of possible mosquito larval control, with *Gambusia* as the active killing agent, indicates the desirability of a knowledge of the changing frequency of the minnow and of the factors that cause this changing frequency. It is the aim of this paper to give a discussion of local and seasonal frequency of the top-minnow as indicated by a study of data collected in a section of the country where *Gambusia* is found in large numbers and where investigations which deal with mosquito and malaria control have been and still are in progress.

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[1] Hildebrand, S. F.: "Fishes in Relation to Mosquito Control in Ponds." Appendix IX to the report of the U. S. Commissioner of Fisheries for 1918. Bureau of Fisheries Document No. 874. Washington, 1919.

FIELD OBSERVATIONS

During the prosecution of this study in the delta region of the Mississippi River at Mound, Louisiana, routine collections of the viviparous top-minnow, *Gambusia affinis,* were made to note relative frequency of the fish for comparison with similar collections of mosquito larvae. These collections, all made by using one-quarter inch meshed seines and dipnets in the bayous, borrowpits, and wood pools of the general vicinity of Mound, oc-

TABLE I. *Seasonal Gambusia frequencies*

Month	Average date of collections	Total fish caught	Number of collections	*Gambusia*									Surface water		Air temperature
				Seine				Dipnet		Total			Average date of measurements	Index	
				Number	Length	Number of fish	Rate per foot	Number	Number of fish	Number	Percent	Rate per collection			
1918															
May...	16	1,043	31	34	629	529	.8	28	42	571	54.7	18.4	9 24	646 587	73.4
June...	15	1,928	31	28	780	1,254	1.6	23	87	1,341	69.5	43.2	10 20	538 442	81.1
July...	11	3,025	31	25	465	2,233	4.8	30	48	2,281	75.3	73.2	5 18	219 184	78.4
Aug....	16	3,442	24	18	337	1,772	5.2	30	25	1,797	52.2	74.9	5 15	121 96	80.1
Sept....	19	1,207	13	9	185	802	4.3	20	1	803	66.5	61.7	13	84	69.4
Oct. ...															67.7
Nov....	26	232	17	12	235	65	.2	43	98	163	70.2	9.5	26	736	52.9
Dec....															51.1
1919															
Jan. ...															44.4
Feb....	25	292	15	14	249	207	.8	5	0	207	70.8	13.7	25	1,425*	50.1
Mar....	26	207	18	12	159	132	.8	31	47	179	86.4	9.9	26	1,460	57.4
Apr....	27	628	22	21	308	227	.7	15	41	268	43.2	12.1	27	1,497	62.9
May...	29	1,054	26	25	532	557	1.0	30	29	586	55.6	22.5	29	1,678	69.3
June...	29	1,642	29	24	433	1,065	2.5	30	72	1,137	69.2	39.2	29	1,359	77.7
July...	25	1,844	31	29	420	1,570	3.7	35	50	1,620	87.8	52.2	25	1,248	80.5
Aug....	27	4,160	31	24	340	3,608	10.6	45	204	3,812	91.6	122.9	27	1,311	81.8
Sept....	16	2,620	29	21	182	1,430	7.8	42	589	2,019	77.0	69.6	16	545	75.6
Oct. ...	17	1,291	25	19	246	748	3.0	41	215	963	74.5	38.5	17	730	72.4
Nov....	14	819	31	22	399	536	1.3	60	87	623	76.0	20.0	14	1,499	58.4
Dec....	6	1,184	31	22	440	457	1.0	50	262	719	60.6	23.1	6	1,534	48.6

* Figures from this point down are the average areas in square feet of twenty-five stations.

curred regularly, when road conditions permitted, at intervals of two weeks from May to November, 1918, and monthly from February to December, 1919. Each general collection contained hundreds of *Gambusia* caught at selected points, numbering twenty-two in 1918 and forty-two in 1919 and representing different environmental features. These collections, summarized monthly, indicate with a fair degree of accuracy the relative frequency of the top-minnow with reference to season and locality throughout the two years. This relative frequency, "rate per collection" of Table 1, rises quickly from a very small rate in winter and early spring to its maximum rate in August, after which it suddenly decreases and returns to the level of the previous winter. The modifying factors of temperature and available water, together with the strictly mathematical considerations of number and length of seine hauls and actual number of fish taken, are included so that the figures may be properly weighted in the discussion. The "surface water index" representing available water has been computed from a study of the various depths of the stations of 1918 and, for 1919, is the average monthly area of twenty-five stations regularly measured. The monthly temperatures tabulated are the monthly average mean temperatures of the air as recorded at the field laboratory of the United States Bureau of Entomology at Mound.[2]

In addition to the above recorded data kept at each collection the sex of each *Gambusia* 1.5 cm. and over in length was noted, the modified anal fin—the intromittent organ of this species—being the character on which the sex of each fish was determined.[3] This determination of sex was made especially to note if different types of environment had any effect on the proportion of sexes in *Gambusia* in succeeding months, since such information seemed desirable from the general viewpoint of the propagation of this species as an agent in mosquito control. The proportion of sexes would, of course, have a considerable effect on the future frequency of the minnow and very possibly on the future frequency of mosquito larvae on which they bring to bear both direct and indirect controlling influence. The varying relative number of males and females in isolated collections of *Gambusia* has attracted some attention in the past.

Dr. H. M. Smith[4] notes that "the proportion of males to females in a lot of specimens of *Gambusia* collected by the writer in Pasquotank River was one to three, but there is usually a greater disparity, the males sometimes representing only two or three percent." S. F. Hildebrand[5] states that "it seems entirely probable that the normal ratio of males to females is about one to eight or nine." Jordan and Evermann[6] note that the males are very scarce, and in a footnote refer to a collection of Dr. H. M. Smith's in the lower Potomac in which there were sixty-eight females and one male. Dr. A. L. Kuntz[7] also notes the disparity in number existing between male and female *Gambusia*.

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[2] The writers were engaged as representatives of the United States Bureau of Fisheries which had entered into cooperation with the United States Bureau of Entomology, and the observations here recorded were made at the field laboratory of the latter Bureau. We are desirous of acknowledging the many kind and helpful suggestions offered us during the prosecution of this study by Dr. W. V. King of the Bureau of Entomology.

[3] *Gambusia affinis* is a dimorphic species in which the adult male is smaller than the female and is easily distinguishable from the adult female because of its prolonged anal fin which is used as a copulatory organ.

[4] Smith, H. M. "Fishes of North Carolina." North Carolina Geological and Economic Survey, Vol. II, 1907, Raleigh.

In the observations at Mound, although we ordinarily found in individual collections a smaller number of males than of females, there were some collections that consisted of a larger number of males than of females: for example, in November, 1918, a collection at our Station 15 gave 26 males and only 14 females. Often in our regular collections there were 30 or 35 percent male fish. On other occasions in catches of fair size we failed to find a male fish, *e.g.*, in a haul at Station 14 during June, 1918, 38 females were taken and no males, and in July at Station 8 we took 125 *Gambusia* of which only one was male. The variability of the ratio of sexes is thus indicated. The effect of this variation, which from our records appears to be quite regular, may also be seen in some cases hereinafter noted.

Numerous studies of the abundance and cause of variation in ratio of sexes have been made in the past. These have indicated that sex determination may be brought about by a large number of possible causes. Adolph H. Schultz,[8] considering sex ratio in man, has cited a long list of literature on the subject. In this literature on the possible causes of variation in sex-ratio the following hypotheses, some disproved, are among those included: time of fertilization, age of parents, nutrition, season, excessive mortality of one sex after birth, inbreeding, race, size of pelvis, hereditary influences, degree of maturation of the egg, and the existence of male- and female-producing spermatozoa. Considering sex-ratio in lower forms there has been much written in recent years. Race-crossing, environmental factors such as available oxygen and kind of food, inbreeding, selection, chromosome combinations, and season have all been shown to have considerable influence on sex-ratio in lower animals.

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[5] Hildebrand, S. F. "Notes on the Life History of the Minnows *Gambusia affinis* and *Cyprinodon variegatus*." Appendix VI to the report of the U. S. Commissioner of Fisheries for 1917. Bureau of Fisheries Document No. 857. Washington, 1917.

[6] Jordan, David Starr, and Evermann, Barton Warren. "The Fishes of North and Middle America." Bulletin 47, U. S. National Museum, Part 1, Washington, 1897.

[7] Kuntz, A. L. "Notes on the Habits, Morphology of the Reproductive Organs, and Embryology of the Viviparous Fish, *Gambusia affinis*." Bulletin U. S. Bureau of Fisheries, Vol. XXXIII for 1913, Bureau of Fisheries Document No. 806. Washington, 1914.

[8] Schultz, Adolph H. "Studies in Sex-ratio in Man." Bulletin Marine Biological Laboratory, Vol. 34, January–June, 1918. Woods Hole, Mass.

In the work at Mound the changing percentage of male *Gambusia* in the total collections for successive months was evident in the summer of 1918. The decrease in the frequency of males was accompanied in one large body of water especially—our Station 14, a borrowpit—with the presence of a non-gravid condition in a large proportion of the females, which condition would not normally occur in midsummer with a proper relative number of males present. This of course pointed to only one of the reasons why such a study is valuable. If such an occurrence should be common to all our pools it was apparent that *Gambusia* frequency would soon be greatly reduced, and, according as the species had been effective mosquito-control agents, so would mosquito larval and adult densities increase. During the years of 1918 and 1919 the proportion of adult males able to copulate varied regularly from season to season, the highest freqency coming in winter and the lowest at the middle of the summer (Table 2). In this table, as throughout this paper unless otherwise specifically noted, *male* indicates a *Gambusia* with the sexual character, the modified anal fin, well developed. The word *female* denotes any *Gambusia* 1.5 cm. or more in length which had not

TABLE 2. *Seasonal male frequency in Gambusia*

Monthly collections of *Gambusia*							
Month	No. of collections	Total No. of *Gambusia*	Males		Young		Average date of collections
			No.	Percent*	No.	Rate per collection	
1918							
May	31	438	73	20.1	76	2.4	16
June	31	724	101	16.5	114	3.6	15
July	31	1,876	191	11.1	158	5.0	11
Aug.	24	582	63	12.8	30	1.2	16
Sept.	13	553	102	18.7	8	.6	19
Oct.							
Nov.	17	132	46	34.8	0	.0	26
Dec.							
1919							
Jan.							
Feb.	16	247	84	34.0	0	.0	25
Mar.	19	179	49	27.3	0	.0	26
Apr.	23	470	86	23.5	104	4.0	27
May	23	785	93	16.1	117	5.0	29
June	28	1,503	219	21.9	287	10.2	29
July	43	1,881	194	13.4	441	10.2	23
Aug.	44	4,528	385	10.6	907	20.6	24
Sept.	38	2,235	478	29.2	601	15.8	14
Oct.	28	1,071	201	20.2	73	2.6	17
Nov.	42	791	189	23.0	28	1.3	13
Dec.	42	785	174	26.7	135	3.2	5
Total, 1918	117	4,305	576	14.7	386		
Total, 1919	344	14,475	2,152	18.2	2,693		

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* Percent of all *Gambusia* 1.5 cm. or over in length.

the male character above noted. *Young* denotes all *Gambusia* under 1.5 cm. in length, with the exception of a very few individuals which, showing the modified anal fin, were classified under the category of *male*. The arbitrary length of 1.5 cm. was set since it was, with rare exceptions, the smallest size at which the male character was evident. The term *Gambusia frequency,* as used in this paper represents the "rate per collection" of all *Gambusia, male, female,* and *young*. All measurements were made from the tip of head to the base of the caudal fin.

Discussion

In the prosecution of this study a total of 18,780 *Gambusia* of all ages has been examined. Of the fish 1.5 cm. and more in length taken in 1918, 14.7 percent were males. In 1919, 18.2 percent were males. The largest monthly percent of males came in November, 1918, and February, 1919, when there were 34.8 and 34.0 percent respectively. The lowest monthly percent of males came in July, 1918, and August, 1919, when there were 11.1 percent and 10.4 percent respectively. Between the period from January to July or August there appears to be a general decrease in the ratio of males to females, even though the actual *Gambusia* frequency continually increases through this period (fig. 1). From August to January of the following year the ratio of males to females has a general increase. Coincident with the decreasing frequency of males from January to August appears an increasing frequency of young *Gambusia* under 1.5 cm. in length.

The observations of 1918 begun in May were upset from July until October by the drouth that prevailed through Northern Louisiana, and that caused many of our stations to dry up or to become very small and shallow. This caused such a concentration of fish in some pools during July that *Gambusia* were sometimes left by the evaporating water on the bare bottoms where snakes and birds fed on them. Collections made at this time in these stations would have given inaccurate ratios, though a large number of *Gambusia* could be taken, and they have therefore been omitted from consideration. There was in the many pools included a sufficiently great number of *Gambusia* to easily indicate, with the help of the surface water index curve (fig. 1) the concentration of fish in these ponds during the period of drouth.

It is possible that in many cases, perhaps in all, some *Gambusia* were lost in the manipulation of the nets. However, inasmuch as such probable error has been common to every collection, the effect on the records tabulated and plotted is minimal. It may be argued that the figures for male fish are not accurate since the small size of males has permitted them to go through the meshes. The table of young *Gambusia* in the 1919 collections shows that the average catch of young—fish under 1.5 cm.—in August was larger than twenty per collection. It seems probable, if it were possible to take young at this rate in any of the collections, that all, or very nearly all, the males

1.5 cm. and over in length which came within the sweep of our nets were captured. However, the aim of this paper is to point out the relations that bring about the varying ratios, and the resulting effect of such ratios on the frequency of the species in nature.

Theoretically it might be expected that the production of the two sexes would be approximately equal. The finding that the females greatly outnumbered the males at all seasons of the year and that the ratio of males to females is a seasonally varying one leads to an inquiry into the causes of this apparently abnormal condition. In this connection there are no data at hand that would indicate that males are less frequent in early spring broods than in summer or fall broods. Further, the rate of growth of male and female from birth to and including 1.5 cm. is not so different that the summer reduction in frequency of males can be attributed to it. The disparity in the rate of growth between male and female comes chiefly after the first six weeks when all *Gambusia,* male and female, will be at least 1.5 cm. in length. The diminishing ratio of males cannot be due, then, to our having included males of a brood among our young, while the females of the brood were classified as adults.

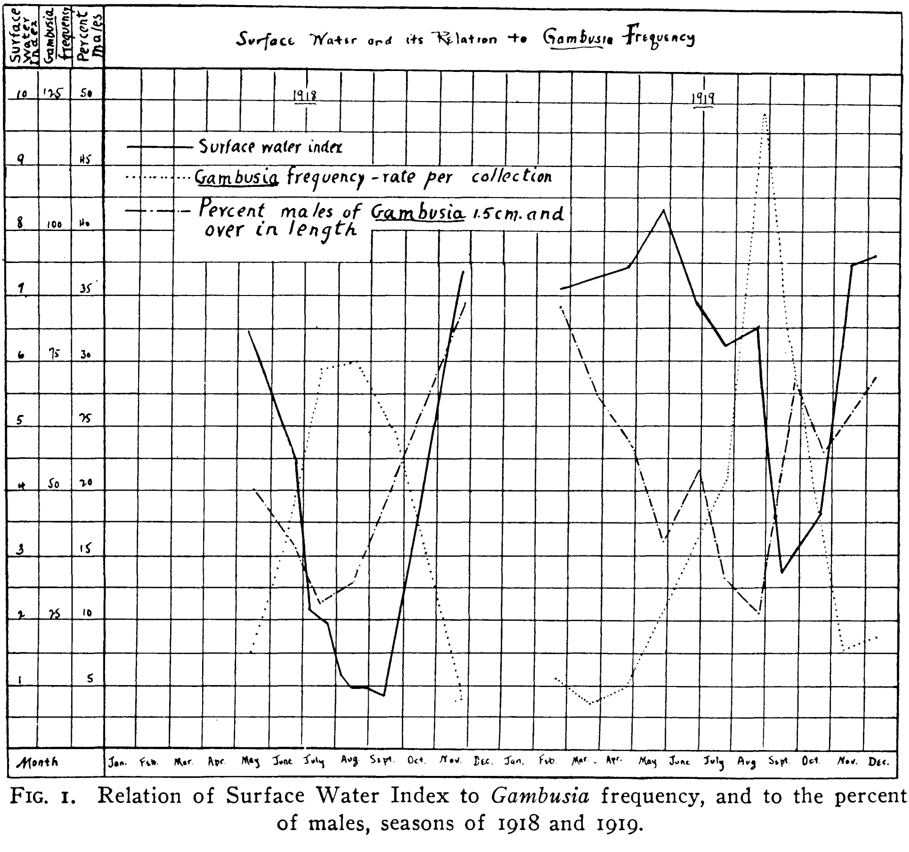

FIG. 1. Relation of Surface Water Index to *Gambusia* frequency, and to the percent of males, seasons of 1918 and 1919.

It might be thought that the higher temperatures[9] produced a high mortality rate in males. This is not the case, however, for in September of each year there is a decided increase in male ratio (see fig. 1), even though the average mean temperature of the air and water of this vicinity is about as high in September as it is in May and June when the male ratio is decreasing. Neither is such mortality probable in view of actual experience. One of the writers in stocking a pond in Alabama in August, 1918, carried several cans of *Gambusia* on a railroad journey of about twenty-four hours, and, on liberating them in the pond found that a large number of adult females had died but no males. This mortality had doubtless been caused by the rapidly increasing temperature of the water in which the fish were shipped. It is evident then that the male *Gambusia* is somewhat more resistant to higher temperatures than the female. That the significance of temperature in this matter is nil is suggested by the fact that the writers have seen on several occasions *Gambusia* thriving with no mortality in pools where the water registered from 97 to 103 degrees Fahrenheit. As Jordan[10] points out, all fresh water fishes in their natural habitats automatically adapt themselves to

TABLE 3. *Male frequency in different environments*

Month	Male frequency in type environments											
	Natural uncleared bayou			Lemna-covered bayou			Impounded water			Borrowpits		
1918 and 1919	*Gambusia* 1.5 cm and over in length	Number of males	Percent of males	*Gambusia* 1.5 cm. and over in length	Number of males	Percent of males	*Gambusia* 1.5 cm. and over in length	Number of males	Percent of males	*Gambusia* 1.5 cm. and over in length	Number of males	Percent of males
Feb...	70*	15	21.4	43*	27	62.7	34*	8	23.5			
Mar..	40*	14	35.0	21*	12	58.0	10*	3	30.0			
Apr...	91*	32	35.1	247†	44	17.8	5*	2	40.0			
May .	252	53	21.0	407†	33	8.1	113	21	18.5	59*	10	16.9
June .	442	87	19.6	172	34	19.0	266	51	19.0	309	46	14.8
July..	639	92	14.3	96	7	7.5	434	86	19.0	5,772†	1,135†	19.6
Aug. .	488	46	9.4	1,016†	118	11.0	378	42	11.1	347*	28	8.0
Sept..	243*	83	34.1	90	33	36.0	320	73	22.0	537*	59	10.9
Oct...	302*	63	20.8	0*	0		13*	0		171*	30	17.5
Nov..	400	102	25.5	65	13	20.0	51	6	11.7	81*	20	24.6
Dec. .	169*	53	31.9	93	24	25.8	107	19	17.8	118*	17	14.4
Total.	3,136	640	20.4	2,250	345	15.3	1,731	311	17.9	7,394	1,345	18.1

* Collections which occurred only in the specified month, 1919, there having been no collections in 1918.

† Includes one very large collection in 1918 omitted in other tables because it was made as pond was about to dry. Included here only because 1919 figures alone would be insignificant.

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[9] The coincident rising of water temperature with air temperature is well indicated in the graph on page 251 in "Life History and Ecology of the Pigmy Sunfish, *Elassoma zonatum*," ECOLOGY, Vol. I, No. 4, 1920. The water there studied is the "*Lemna*-covered Bayou" of this study.

[10] Jordan, David Starr. "Guide to the Study of Fishes," Vol. I, p. 149, New York, 1905.

increasing seasonal temperatures and are little sensitive to climatic temperature changes.

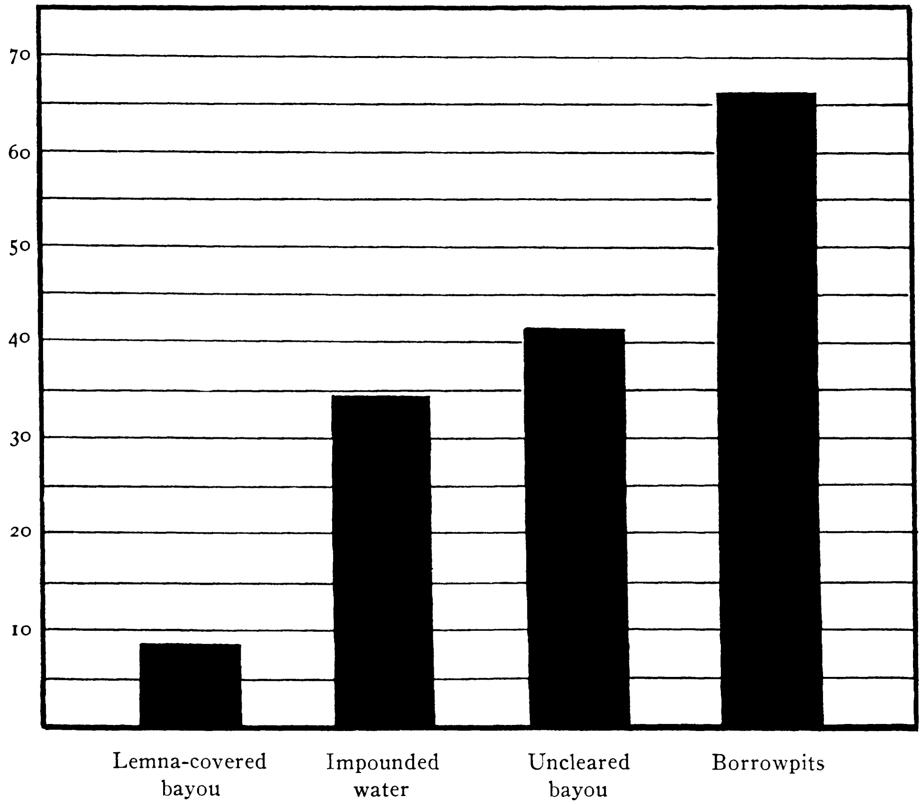

FIG. 2. *Gambusia* frequency in different environments. Observations for 1918 and 1919 combined. Frequency expressed as rate per collection.

The effect of type environments, differentiated by their floral, faunal, and physical features especially, on the seasonal ratio of sexes in *Gambusia* is, from our observations, insignificant, since each of the environmental divisions presents approximately the same seasonal ratios (Table 3). The relatively few fish taken in these environmental divisions, consisting in from three to six stations, has led us to combine both seasons' observations and give totals for each month from collections of both years. In some cases the totals for both years are so small that they are misleading and could be very well excluded. They are, however, included in the table of totals and have been plotted with those figures which are large enough to give a fair index of true ratios. It will be noted from the relative *Gambusia* fre-

TABLE 4. *Gambusia frequency in type environments*

Environmental type	Number of collections*	*Gambusia*							
		Seine				Dipnet		Total	
		Number	Length in feet	Number of *Gambusia*	Rate per foot	Number	Number of *Gambusia*	Number of *Gambusia*	Rate per collection
Natural uncleared bayou	162	139	2,078	6,068	29.2	161	725	6,793	41.9
Impounded water	82	88	1,729	2,817	16.2	0	0	2,817	34.3
Lemna-covered bayou	41	2	20	16	.8	206	342	358	8.7
Borrowpits	51	52	1,203	3,398	28.2	0	0	3,398	66.6

quency of these environments that certain of them are apparently more conducive to *Gambusia* life than others, and contain a greater relative number of *Gambusia* (fig. 2). Although this difference in frequency in different environments is true, there is little variation in the seasonal ratios of males among them (figs. 3 and 4), nor is the total percent of males much different in the varying environments. It appears quite evident then, that environment in this case has an insignificant effect on seasonal variation in sex ratio, though it is apparent that it has a considerable influence on the abundance of the minnow. In the Lemna-covered bayou (see fig. 1, ECOLOGY. Vol. I, No. 4, p. 244, 1920) the *Gambusia* rate per collection was 8.7 for

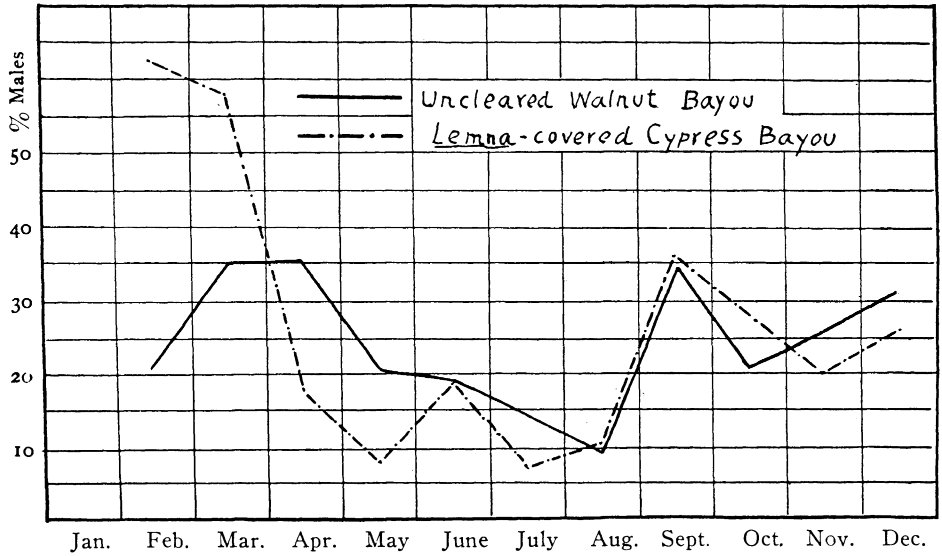

FIG. 3. Seasonal male frequency in Lemna-covered Cypress Bayou and uncleared Walnut Bayou. Observations of 1918 and 1919 combined. Frequency expressed in percent of males for all *Gambusia* 1.5 cm. and over in length.

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* Collections of 1918 and 1919 combined.

1918 and 1919, while in the borrowpits (open ponds resulting from excavations for levee construction) and the "natural bayou" stations (points along sluggish bayous which were "wild" or only partly cleared, fig. 5) the rates per collection for the two years were, respectively, 66.6 and 41.9. The impounded water station (points along a dammed-up body of water from which all aquatic vegetation had been removed) yielded for the two years a *Gambusia* frequency of 34.3.

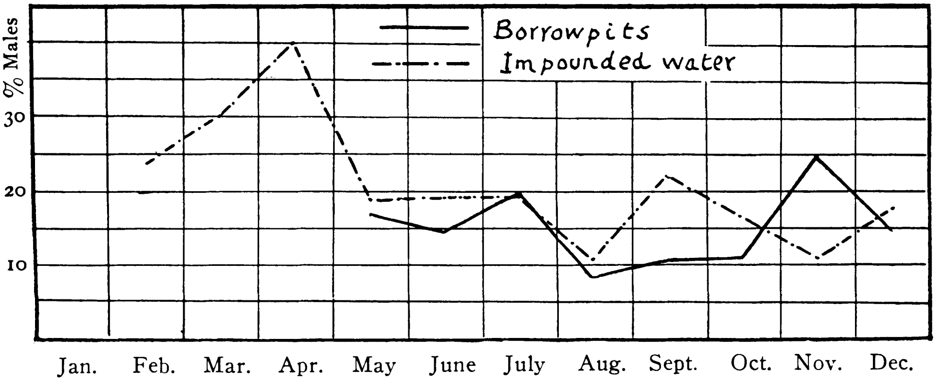

FIG. 4. Seasonal male frequency in impounded water and borrowpits, 1918–1919 combined.

This elimination of possible environmental features in changing the seasonal ratio of sexes throws out with it such considerations as water temperature, food, oxygen content of water, etc., which might have been thought to bear considerable significance to the subject. That these same factors do have, however, a notable influence on the production of *Gambusia* is evident from certain studies on the propagation of the minnow.[11] On the basis of the studies here cited, and of our knowledge of the total biological differences of the environmental types above referred to, we feel at liberty to conclude that the above mentioned environmental features were nil in their effect on the changing seasonal ratio of sexes. Yet there are considerable physical, faunal, and floral differences, and the fish of these environments, both in actual abundance and in species other than *Gambusia* present, are also quite different. The presence of such animals as prawn, backswimmers, and protozoa in surface scums of certain environments, and their total absence or negligible occurrence in others, further emphasizes the unlikeness of the environments. It is significant in this connection that the environments differed in source, turbidity, and temperature of their waters and in their flora.

Further inquiry into the causes of the varying seasonal frequency of males and of the species, shows that with each summer there is a decrease in depth and area of all water systems studied (fig. 1). This is due to increased evaporation caused by the higher temperatures of the summer, coincident with the light summer rainfall, and also to increased seepage of water from the bayous, ponds, and pools into the Mississippi River which during the summer is usually at a low stage. This lowering of the water in the bayous and ponds eliminates all the shallow margins which *Gambusia* frequent and where they are largely immune from their enemies, and forces the fish into deeper water where the incline of the banks is steeper. This accordingly means much less natural protection than the minnows formerly had, since predaceous fish, now at a period of heightened metabolism and consequent rapid growth, are especially destructive and have a marked effect in lowering *Gambusia* frequency. Doubtless the *Gambusia* eaten by their predators at this time are nearly all females of large size, since the adult females, gravid at this season, are much larger, much slower in movement, and are more noticeable because of their black abdominal spots than the small, quickly moving, uniformly colored males. With the height of *Gambusia* frequency in late August (1919) occurs properly the height of the young *Gambusia* frequency. The young frequency then diminishes quickly, apparently due to the scarcity of breeding males during the spring and summer, and the resulting lowered birth rate. The height of *Gambusia* frequency is immediately followed by a considerable drop in water stage (surface water index) and accompanied by an increase in the percentage of other species, many of which are predators (Table 1). The *Gambusia* frequency decreases by loss of adult females, while the male frequency accordingly

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[11] The study here referred to deals with the effect of dissolved oxygen and aquatic plant life and their bearing on the propagation of *Gambusia* in small ponds. This investigation is now in preparation for publication.

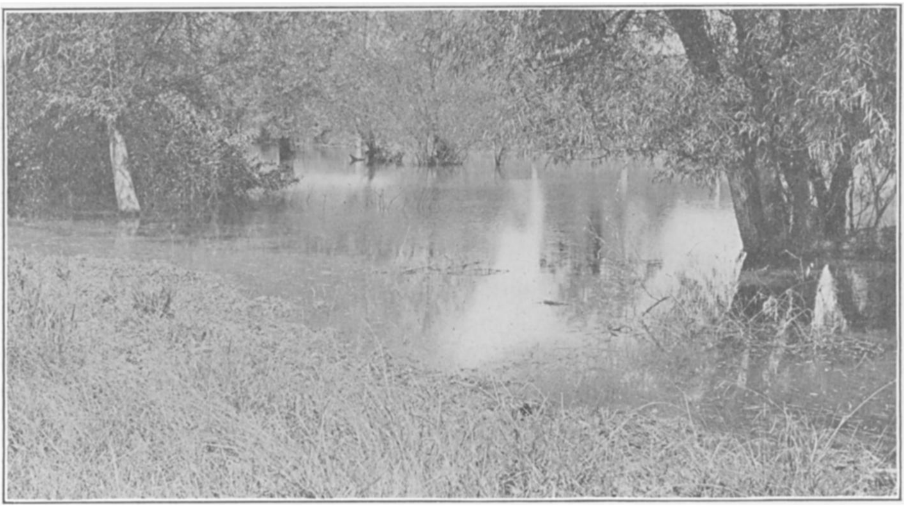

FIG. 5. Walnut Bayou, an uncleared bayou.

increases. The decided and perhaps abnormal prevalence of males in the September (1919) collections is well explained by the fact that the surface water had suddenly been diminished by more than half, thus quickly bringing into the category of food many large females which otherwise would have continued to live and breed, keeping the male ratio lower.

In further explanation of the causes of the varying sex-ratio and its bearing on *Gambusia* abundance we are indebted to Dr. S. O. Mast of Johns Hopkins University who has very kindly given us information that adds much to the above explanation of portions of the male and *Gambusia* frequency curves.

Dr. Mast has noted that there is a decided tardiness in the development of the male sex character—the modified anal fin. It appears that this modification of the anal fin occurs as a true secondary sexual character. Dr. Mast, discussing certain *Gambusia* he had in his laboratory during the winter of 1918–1919, writes as follows: "In looking these over I found among the smaller ones almost no individuals having male characteristics. Now these were evidently born in the autumn toward the close of the season. Among the largest of the individuals seen there were about six times as many females as males, that is, six times as many individuals having the external female characteristics as individuals having external male characteristics. I separated those which I thought were males from those which I thought were females and kept them in separate tanks and later in the winter I discovered in the tank which was supposed to contain nothing but females a considerable number of individuals which had definite male characteristics. These were removed, but later in the season I again found a considerable number of males, so that it is evident that the male characteristic may develop after the fishes have attained a fairly good size."

Applying this fact to our male frequency curve we find that it correlates well with our recorded observations. The continued decrease in the proportion of males to females through the spring and the summer to August is easily conceivable in view of the tardiness of the development of the male secondary sexual character. From our curve it appears that the frequency of males increases from August on. This upward trend of the curve is due then, in addition to the effect predaceous fish may have in killing off females, to the increasingly large number of *Gambusia,* previously classified as females because of the unmodified anal fin, coming to sexual maturity and developing the external sexual character of the male. The arrival at sexual maturity of a large number of the males produced during the spring and early summer is well indicated by the marked upward movement of the male frequency curve in September (1919). The similar, though not so decided, upward movement of the young curve (fig. 1) in December, 1919, is a nice indication (unseasonably warm weather happily occurring during October and November) of the effect of the marked increase in male frequency in

September. The greater prevalence of males during September and the consequent fertilization of the already abundant females, many non-gravid because of dearth of males up to this time, caused the increase in young noted above. This is reasonable, since from Seale's[12] observations we learn that the average period of gestation of five broods released between December 8, 1915, and June 23, 1916, is 39+ days. These observations, carried on in the Philippines, were made on a fish kept in a laboratory aquarium and it is probable that this average period of gestation is somewhat shorter than occurs in nature in northern Louisiana.

With continuous years of warm breeding weather with no upsetting drouth, diseases, predators, no limitations as to surface water, we might expect the male frequency curve, as recorded here, and our young frequency curve (fig. 1) to be continuous wavy curves with each crest mounting increasingly higher. As it is, with the existing balance of nature and with the intervening temperatures of winter to retard growth and breeding, and with low winter survival, there is once each year a gradual falling and rising of the curves representing *Gambusia* frequency and proportion of sexually mature males. Winter survival of *Gambusia* is well illustrated, and the effect of winter temperatures on decreasing *Gambusia* frequency can be better understood, by outlining a study carried on during the winter of 1917–1918. A pond, 36 by 9 feet and with depth varying between 7 and 18 inches, was stocked on August 31, 1917, with 1,732 *Gambusia,* including 28 adult females; a second pond of approximately the same dimensions was stocked with 2,244 *Gambusia,* including 49 adult females. In May, 1918, there were recovered from these ponds, even though there must have been some production of young *Gambusia* during the fall of 1917, only 651 and 499 fish, respectively. This winter was especially severe for Northern Louisiana.

The young curve, beginning with a frequency of close to zero in late winter, rises gradually to about the first week in September and then takes an abrupt fall, at which level it continues till cold weather brings it down again nearly to zero—the very few late fall broods making it possible to find *Gambusia* under 1.5 cm. in length in almost every month of the year. The sudden decrease in young frequency in September cannot be due to lower water temperature retarding the embryonic development of the many *Gambusia* carried *in utero* at this season, for there existed in October and November (1919) temperature conditions fully as conducive to prolific breeding as had existed in late spring when young frequency was increasing. Neither can this sudden decrease be due to the fact that the pools and bayous had reached their fish-supporting capacities, since in August, a warmer month, when dissolved oxygen capacity was smaller, there had been twice as many fish present. Water levels were lower in September, but at all times during 1919 there was abundant water in all but a few of our stations, and it is improbable that the ponds held their capacities in September. The obvious cause of the abrupt fall of the young curve in September is, then, the low male frequency of the early summer, there not having been sufficient males to impregnate all the females at that time.

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[12] Seale, Alvin. "The Mosquito Fish, *Gambusia affinis* (Baird and Girard) in the Philippine Islands." Philippine Journal of Science, Vol. XII, No. 3, Section D, May, 1917. Manila.

Further cause of the changing *Gambusia* frequency and sexratio, though its significance and importance to this subject is still unknown, is the appearance among individuals of this species of sterile males, which, though they have testes, have not the modified external sexual character. These, though males, have been counted heretofore as females, since the character —the prolonged anal fin—by which observers could have determined the sex had never been developed. Regarding this condition, Dr. S. O. Mast writes: "I have made rather extensive studies of certain phases of the problem and I find that frequently there are among the individuals which externally are precisely like females, that is individuals in which the anal fin is like that which is found in typical females, some that contain testes. These individuals are consequently males although, of course, they are sterile. Thus it is evident that many of these fishes which have ordinarily been counted as females are in reality sterile males, and the sex ratio as reported is probably not at all correct."

Such a condition is not at all infrequent in other dioecious species and, as Castle[13] has pointed out, is the result of the typical working of Mendel's law involving the principles of dominance and segregation. He points out that "the ordinary dioecious individual is a sex hybrid of 'heterozygote' in which the characters of both sexes are present, one dominant, the other recessive. In the male the female character is recessive, and, conversely, in the female, the male character is recessive; but each sex transmits the character of both." Cuenot[14] has indicated the difficulty of observing the sex of individual frogs by external appearances. He notes that certain frogs which externally had male characters were, from examination of their internal sex organs, females. Convincing evidence of the latency of one sex in the other has been brought to light in recent years by Goldschmidt[15] in his studies on the gypsy moth. He has been able to show the existence of intergradations between sexes in this moth. That such intersexuality is common throughout the animal world is suggested by the fact that sex intergrades have been noted in the entomostracan *Daphnia*. In this connection we may cite the finding of shad occasionally which, though having external male appearances, contain ovaries.[16]

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[13] Castle, W. E. "The Heredity of Sex." Bulletin Museum of Comparative Zoology at Harvard College, Vol. XL, No. 4, Cambridge, Mass. January, 1903.

[14] Cuénot, L. "Determination du sexe." Bulletin scientifique de la France et de la Belgique; 32, 5e series, 1, 1899.

[15] Goldschmidt, Richard. "Experimental Intersexuality and the Sex-problem." American Naturalist, Vol. 50, 1916.

[16] Fowler, H. W. Science, N. S., Vol. XXXVI, No. 914, p. 19, 1912.

SUMMARY

Among other factors essential to biological control of immature mosquitoes, there is the important requirement of an abundance of *Gambusia affinis,* the top-minnow and usual destructive factor of an environment in which biological control is attempted. The possible economic value of the top-minnow as an agent of control in the mosquito and malaria problem has prompted this study, for a knowledge of the normal life conditions of *Gambusia* is of importance in any practical effort to use the minnow as an agent in a mosquito extermination campaign. The following conclusions seem to be warranted from the data here published:

1. *Gambusia* frequency varies seasonally in the bayous, borrowpits, and wood pools of the vicinity of Mound, Louisiana. The frequency increases rapidly from late April to July or August when a gradual decrease begins and continues through the fall to bring the frequency back to its normal winter level. The varying *Gambusia* frequency depends on prolific spring and early summer production to bring it to its maximum point. The late summer and fall decrease is brought about by lowering water levels and consequent diminishing natural protection against predaceous fish, together with a decreasing production of young—the result of the decreasing proportion of sexually mature and potent males during the previous spring. Winter temperatures also lower the frequency by causing a high death rate during the colder months.

2. The frequency of male *Gambusia* with the anal fin developed, and sexually potent, varies regularly throughout the year. This changing proportion of males to females in collection records is due in part to a tardiness in the development in the male of the secondary sexual character, the prolonged anal fin, and in part to the increased mortality rate among adult females during the late summer and fall coincident with lowering water levels. The production of sex intergrades in *Gambusia* broods may also have an important bearing on the changing male ratio and very possibly on *Gambusia* frequency. The changing proportions are partly real and partly apparent.

3. The ecological factors, food, temperature of water, dissolved oxygen content, and vegetation, as represented by different type environments studied in this connection, may govern the abundance of *Gambusia* in those type environments, but do not effect the general seasonal trend of the curves representing *Gambusia* frequency and male frequency.